

GREAT HORNED AND BARN OWLS PREY DIFFERENTIALLY ACCORDING TO THE AGE/SIZE OF A RODENT IN NORTHCENTRAL CHILE

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ABSTRACT.—Based on cranial measurements we estimated the size- and age-class (juvenile or adult) of leaf-eared mice (*Phyllotis darwini*) consumed by great horned (*Bubo virginianus*) and barn owls (*Tyto alba*) during 1990–92 in a semiarid locality of northcentral Chile. We compared this information to that obtained from mice live-trapped at the same place and period. The frequency distributions of body weights of leaf-eared mice consumed by the two owl species was not statistically different, despite the four-fold difference in body size and different hunting mode of the two owls. In two out of three breeding seasons the owls preyed more frequently on adult mice. In the remaining breeding season and the three wintering seasons they preyed upon adults and juveniles in about the same proportion as they were live-trapped in the field. The higher predation on adult individuals (reproductive) was associated to a greater mobility of adult versus juvenile mice, which may render the former more vulnerable to owl detection.

KEY WORDS: *Bubo virginianus*; Chile; mediterranean ecosystem; *Phyllotis darwini*; predator selectivity; prey vulnerability; *Tyto alba*.

Tucúqueres y lechuzas depredan diferencialmente de acuerdo a edad/tamaño de un roedor en el centro-norte de Chile

RESUMEN.—Sobre la base de medidas craneanas, estimamos las clases de tamaño y edad (juvenil o adulto) de ratones orejados (*Phyllotis darwini*) consumidos por buhos (*Bubo virginianus*) y lechuzas (*Tyto alba*) durante 1990–92 en una localidad semi-árida del centro-norte de Chile. Esta información la comparamos con aquella obtenida de ratones trampeados en vivo en el mismo lugar y período. Las distribuciones de frecuencias de tamaños corporales de ratones orejados consumidos por buhos y lechuzas no fueron estadísticamente significativas, a pesar de la diferencia cuádruple en tamaño corporal y el diferente modo de caza entre buhos y lechuzas. Durante dos de las tres estaciones reproductivas, buhos y lechuzas depredaron más frecuentemente sobre ratones adultos. En la restante estación reproductiva y las tres estaciones de invernada, ellos depredaron sobre ratones adultos y juveniles en aproximadamente la misma proporción en que fueron trampeados en terreno. La mayor depredación sobre ratones adultos (reproductivos) estuvo asociada a una mayor movilidad de los adultos versus los juveniles, lo que puede hacer a los primeros más susceptibles a la detección por parte de buhos y lechuzas.

[Traducción Autores]

Studies of predator-prey relationships among terrestrial vertebrates have received considerable attention. These studies have focused mainly on raptorial birds and carnivorous mammals as predators, and small mammals as their prey (see Jakšić and Simonetti 1987, Marti 1987 for reviews). A persistent objective has been to determine the impact that these predators have on their prey (Sih et al. 1985). Considering prey populations as the target of predation studies, a priority should be to determine whether there is selective predation on different age/size classes (e.g., juveniles or adults) or sexes (Blondel 1967, Marti and Hogue 1979, Zamorano et al. 1986,

Longland and Jenkins 1987, Vargas et al. 1988, Dickman et al. 1991).

In the semiarid locality of Aucó (northcentral Chile), the nocturnally active leaf-eared mouse (*Phyllotis darwini*) is the most abundant small mammal (Jiménez et al. 1992). Leaf-eared mice are the most common prey of the local predator assemblage, both in periods of high and low mammal abundance (Jakšić et al. 1992). Here we aim at establishing the relative vulnerability of different age/size classes of leaf-eared mice to predation by the two most common local owls, great horned (*Bubo virginianus*) and barn owls (*Tyto alba*).

MATERIAL AND METHODS

Study Area. Las Chinchillas National Reserve (31°31'S, 71°06'W), at Aucó, is located approximately 300 km north of Santiago, Chile. This region has a semiarid mediterranean climate (di Castri and Hajek 1976). Mean annual precipitation is 175 mm, 85% of which is concentrated from May to September (austral winter). Elevations range from 400–1700 m, and the slopes have a vegetation that depends on solar exposure. On equator-facing slopes, vegetation is dominated by cacti such as *Trichocereus* sp., bromeliads such as *Puya berteroniana*, and evergreen shrubs such as *Bahia ambrosioides*, *Cordia decandra*, *Bridgesia incisaefolia* and *Flourensia thurifera*; on polar-facing slopes, the evergreen shrubs *Adesmia* sp., *Porlieria chilensis*, *Colliguaya odorifera*, and *Proustia* sp. are the dominant species.

Abundance of Leaf-eared Mice. From March 1990 to February 1993, we monitored leaf-eared mouse population abundance. Through mark-recapture procedures (using numbered ear-tags), every month we determined the abundance/ha (minimum number known alive; Krebs 1966) and size distribution (body mass) of leaf-eared mice. To capture them, we set four trapping grids, two each on opposite slopes of two creeks where great horned and barn owls roosted and/or nested. Each grid had 7 × 7 trap stations set 15 m apart, which were equipped with one Sherman live trap (8 × 10 × 23 cm). The trapping surface of each grid was 1.1 ha. The traps were continuously present at the four grids, to minimize disturbance, and were activated and baited with rolled oats only during the trapping sessions described as follows. The two opposite-facing grids (2.2 ha) of each creek were simultaneously live-trapped for five consecutive nights (traps were checked the following morning) in alternate months. The reason for alternating trapping between creeks on a monthly basis was two-fold: shortage of manpower to keep simultaneous trapping in the two creeks, and need of replication. Other characteristics, shortcomings, and merits of the trapping scheme used are described at length by Jiménez et al. (1992). This methodology is assumed to provide an unbiased estimate of abundance and age/size structure of leaf-eared mice because of the ease in trapping this rodent in Aucó and nearby localities (80–100%, Simonetti 1986). Each individual captured was weighed and classified as juvenile or adult. At Aucó, leaf-eared mice generally reach reproductive maturity at 40 g (when ca. 50% of mice were reproductive; $N = 551$, unpubl. data). Therefore we established this weight threshold for distinguishing between juveniles and adults.

Predation by Owls. Concurrent with the monthly trapping sessions, we collected pellets of great horned owls (*Bubo virginianus*) and of barn owls (*Tyto alba*) under perches, roosts and nests in Aucó. At least one pair of great horned and four of barn owls were inhabitants of the study area. The pellets were at most 1-mo-old, because we paid monthly visits to the places frequented by the owls. We analyzed pellet contents in the laboratory to determine the respective diets of the two owls at the study site. Prey remains in pellets (mostly small mammals) were determined to species level. More details about procedures may be found in Jaksic et al. (1992). Whole cranial remains of leaf-eared mice found in owl pellets were set apart and

measured. According to the morphometric characters of each cranium, we estimated the body mass and age class. Unfortunately, we did not record the sex of specimens in owl pellets.

The relationship between cranial measurements and body mass (BM) was calculated from data at the Museo Nacional de Historia Natural (Santiago, Chile). The two cranial dimensions used were: maximum distance between nasal and occipital bones over the dorsal side (NOL), and minimum distance between upper incisor and first molar (IML). These measurements were called basilar length and upper diastema, respectively, by Blem et al. (1993). The respective regression equations that we obtained were ($N = 23$ and 21 , respectively):

$$\text{BM} = \text{Antilog} [(NOL - 0.279447)/1.068342]$$

$$\text{BM} = \text{Antilog} [(IML + 0.072450)/0.514116]$$

These two equations yielded significant correlation coefficients ($r = 0.95$ and 0.89 , respectively; both P s < 0.05). The first one was used when whole crania were retrieved from pellets, the second when only snouts were recovered intact. By using this complementary approach to determine body mass of mice, we expected not to overestimate representation of adults (or underestimate that of juveniles) in owl diets, owing to the observed lower breakage of adult crania in the pellets (see also Blem et al. 1993). Because snouts of both adults and juveniles were retrieved mostly intact, we think that our estimates of age/size class proportions are relatively free of bias.

Statistical Analyses. We applied bilateral Kolmogorov-Smirnov tests (Sokal and Rohlf 1981) to compare the size distribution of leaf-eared mice preyed upon by each species of owl. Although estimates of body mass obtained from cranial measurements are accurate to 1 g, we preferred to group individuals into 10-g increment classes because of the inherent statistical error contained in making extrapolations based on regressions. For this part of the analysis we pooled data obtained during the entire study period of 36 mo (March 1990 to February 1993).

To determine if owls preyed selectively upon certain age/size classes of leaf-eared mice, we compared the frequency of different age/size classes observed in the respective owl diets with that expected from observed trapping results. In this case, data were grouped and analyzed according to breeding (September to February) and wintering seasons (March to August) in each of 3 yr. The breeding season of great horned and barn owls roughly corresponds to that of leaf-eared mice, except for the fact that the owls reproduce only once during the season, whereas the mice usually produce two or three litters. Males of leaf-eared mice become scrotal and females perforate in August. It is possible to trap juveniles in November, and by February no males have scrotal testes and only a few females show signs of being pregnant (Fulk 1975). The wintering season is the same for both owls and mice. The statistical comparisons were effected by means of chi-square tests (Sokal and Rohlf 1981), separately for juvenile and adult rodents. Significant differences would thus indicate that some prey class was over- or underrepresented in owl diets, whereas lack of significance would mean that consumption of prey classes was in about the same proportion as they occurred in the field.

RESULTS

Barn owls consumed leaf-eared mice of a mean mass of 54 g (SD = 13; $N = 287$) with a range 20–89 g, whereas great horned owls preyed upon individuals with a mean mass of 50 g (SD = 15; $N = 353$), with a range 10–89 g (Fig. 1). Bilateral Kolmogorov-Smirnov tests did not yield any statistically significant differences in the prey size distributions consumed by the two owl species for any of the six seasons included in the study period (D s from 0.101 to 0.286, all P s ≥ 0.10).

From the wintering season of 1990 (March to August) to the breeding season of 1992 (September 1992 to February 1993), we captured 664 individuals of leaf-eared mice. Throughout all six biological seasons (= 36 mo), adult individuals were captured more frequently than juveniles. Adults accounted for 55–80% of total captures, whereas juveniles represented 20–45% of the captures (Table 1).

Except for the breeding seasons of 1990 (when only the great horned owl was at the site) and 1992 (when the two owl species were present), both owls preyed upon adult and juvenile leaf-eared mice in about the same proportion as they were live-trapped in the field (Table 2). In the two seasons where differential predation was recorded, adults were overrepresented and juveniles underrepresented in the owl diets.

DISCUSSION

The body size distribution of leaf-eared mice individuals preyed upon by the two owl species was not significantly different. This similarity is interesting considering the four-fold larger mass of great horned owls (ca. 1200 g) compared with barn owls (ca. 300 g), and their different hunting modes: the former is a sit-and-wait predator that hunts from elevated perches and the latter is an active-search forager that hunts while in flight. In this respect it is also interesting that Jakšić and Carothers (1985) showed that differences in foraging mode by owls were not reflected in trophic attributes such as mean prey size. Our results support their conclusion.

In four out of the six seasons analyzed at Aucó, our results show that predation by great horned and barn owls was proportional to the respective abundance of each age/size class of leaf-eared mice. In two out of the three breeding seasons analyzed, adult leaf-eared mice occurred in higher frequencies in owl diets than did juveniles.

What determines differential predation on differ-

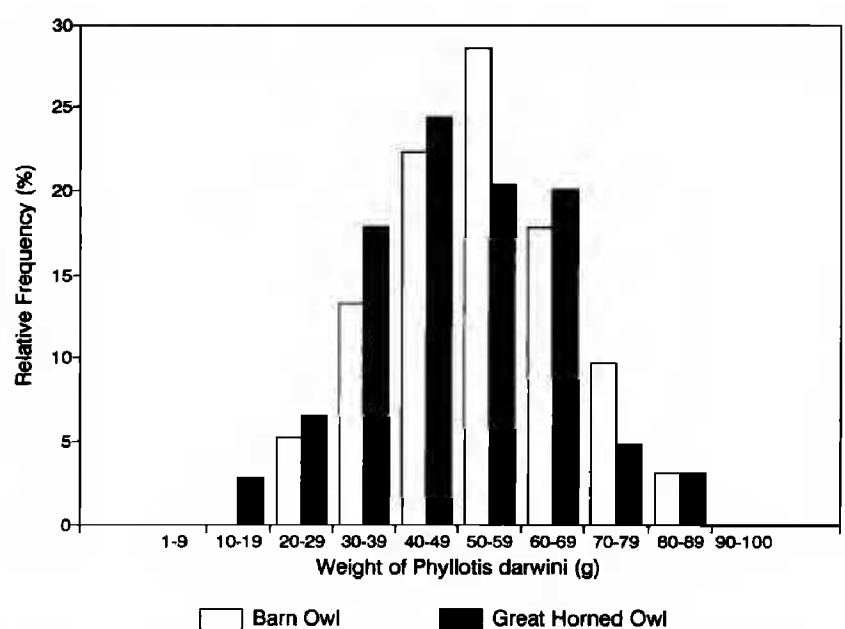


Figure 1. Weight frequency distribution of leaf-eared mice (*Phyllotis darwini*) consumed by great horned (*Bubo virginianus*; $N = 353$ mice) and barn owls (*Tyto alba*; $N = 287$ mice) in Aucó, northcentral Chile, 1990–92.

ent age/size classes? Several authors (e.g., Zamorano et al. 1986, Vargas et al. 1988) have concluded that preferential consumption of certain prey sizes shows that predators are capable of discriminating, presumably selecting those that yield the highest energy benefit/cost ratio. However, it is difficult to determine whether predators indeed select prey of certain size or age, or are simply taking those classes that are most vulnerable.

Many studies have shown that differential prey vulnerability determines disproportionate predation upon some prey classes (e.g., Errington 1956, Metzgar 1967, Lay 1974, Marti and Hogue 1979). For instance, Longland and Jenkins (1987) noted that great horned owls preyed mostly on juveniles of mon-

Table 1. Composition (%) by age of leaf-eared mice (*Phyllotis darwini*) as estimated by live-trapping in Aucó, northcentral Chile. W = wintering season (March to August); B = breeding season (September to February); Juveniles <40 g; Adults ≥ 40 g.

AGE CLASSES	SEASON					
	W 1990	B 1990	W 1991	B 1991	W 1992	B 1992
% Juveniles	37.5	45.3	20.3	40.4	28.4	33.9
% Adults	62.5	54.7	79.7	59.6	71.6	66.1
MNKA ^a	47	85	60	262	81	124
Number/ha	10.7	19.3	13.6	59.5	36.8	56.4

^a Minimum number known to be alive during the period stated.

Table 2. Observed (Obs) and expected (Exp) absolute frequencies of juvenile and adult leaf-eared mice (*Phyllotis darwini*) in the diets of great horned owls (*Bubo virginianus*) and barn owls (*Tyto alba*) in Aucó, northcentral Chile. W = wintering season (March to August); B = breeding season (September to February); n.t. = not testable because of zero cell frequencies.

AGE CLASSES	SEASON											
	W 1990		B 1990		W 1991		B 1991		W 1992		B 1992	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
<i>Bubo</i>												
Juveniles	11	17	2	8	0	1	55	59	27	32	1	9
Adults	35	29	16	10	5	4	91	87	84	79	26	18
<i>P</i> (χ^2)	>0.05		<0.005		n.t.		= 0.45		>0.25		<0.001	
<i>Tyto</i>												
Juveniles	11	14	0	0	0	1	8	12	26	30	8	37
Adults	27	24	0	0	7	6	21	17	79	75	100	71
<i>P</i> (χ^2)	>0.25		n.t.		n.t.		>0.10		>0.25		<0.001	

tane voles (*Microtus montanus*) and attributed the higher mortality of juveniles to higher dispersal rates and lack of experience or sensory skills to avoid owl predation. Dickman et al. (1991) found that barn owls preyed mainly on the smaller size classes (presumably juveniles). They proposed that juvenile house mice (*Mus domesticus*) were more heavily preyed upon because they were displaced by adults into open patches, where predation risk was greater. On the other hand, Kotler (1985) and Kotler et al. (1988) found that the rodent species most consumed by barn owls were those (pocket mice [*Perognathus* sp.] and deer mice [*Peromyscus* sp.]) that foraged under or near shrub cover, used quadrupedal (slower) locomotion, and had smaller body mass than kangaroo rats (*Dipodomys* sp.), which foraged in open areas, were bipedal (faster), and of larger size. Blem et al. (1993) found that subadult voles (*Microtus pennsylvanicus* and *M. montanus*) were more frequently preyed by short-eared owls (*Asio flammeus*) than expected from snap-trapping, and attributed it to dispersing juvenile voles being more vulnerable than resident adult voles.

In Fray Jorge, a locality about 100 km to the northwest of our study site, Fulk (1976) found that adult leaf-eared mice were overrepresented in the diet of barn owls. He attributed this finding to an artifact of comparing trapping data obtained in mid-November with a pellet accumulation dating back to mid-August. Fulk (1976) reasoned that there were no juveniles available to barn owls before November (when the former joined the free-ranging population), and thus more adults were found in the pellet

sample than in the field. In our study area, lag between trapping and pellet accumulation was not a major factor, as pellet collections and trapping sessions were evenly spaced on a monthly basis. In addition, pooling of data into 6-mo intervals diluted the influence of the first event of juvenile recruitment into the trappable population of leaf-eared mice. Further, overrepresentation of adults occurred when least expected, during breeding seasons, when juvenile abundance peaked in comparison to preceding wintering seasons.

Why should adult leaf-eared mice be more vulnerable to predation by great horned and barn owls during breeding seasons at Aucó? Both adults and juveniles have the same dispersal capability at the site (P.A. Marquet unpubl. data). Unless one invokes larger size as the key used by owls to prey disproportionately more on adults (e.g., Bozinovic and Medel 1988, Jaksic 1989), only traits associated with reproduction are left as factors. Perhaps reproductive males in search of females are less cautious or move more within their home range, or gravid females are slower at escaping predation attempts. With the data at hand we cannot resolve these questions, which remain as stubborn blocks in our general understanding of the cues used by predators to hunt and of the attributes that render some of their prey more vulnerable than others.

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